Trisecodes gen. n., (Hymenoptera: Eulophidae: Entedoninae), the First Eulophid with Three Tarsal Segments

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Abstract.—The neotropical genus *Trisecodes*, and its type species *T. agromyzae*, are described in the eulophid subfamily Entedoninae. Its placement within the Chalcidoidea and the Eulophidae is discussed. Its hosts, all belonging to Agromyzidae (Diptera) are listed. This is the first Eulophidae, as well as the first member of the Chalcidoidea outside of the Trichogrammatidae, where both sexes have three tarsal segments.

Résumé. Les auteurs décrivent le nouveau genre néotropical *Trisecodes*, ainsi que son espèce type, *T. agromyzae*, dans la sous-famille des Entedoninae (Eulophidae). Ils discutent ensuite de sa position systématique à l'intérieur des Chalcidoidea puis des Eulophidae. Ils citent les hôtes de cette espèce, qui appartiennent tous à la famille des Agromyzidae (Diptera). Il s'agit du premier Eulophidae, mais aussi du premier chalcidien n'appartenant pas aux Trichogrammatidae, dont les deux sexes présentent des tarses trimères.

Understanding the evolution of the superfamily Chalcidoidea, and deriving robust phylogenetic hypotheses, is a major challenge. The difficulty comes from the biodiversity of the group, one of the most speciose superfamilies of the Hymenoptera (Noyes 1998), and the plasticity of both morphological and biological features exhibited by these wasps (Gibson 1990; Gibson et al. 1999). The genus described below is an example of such plasticity. Up to now, the only Hymenoptera known to have 3-segmented tarsi were members of the family Trichogrammatidae, and some highly derived and dimorphic male fig wasps (Agaonidae). The presence of three tarsal segments in both sexes has been considered a synapomorphy for the Trichogrammatidae, many of whose members also have lines of setae on the forewing. The wasp described in this paper, Trisecodes agromyzae, shares these features with the Trichogrammatidae but does not belong to this family.

Specimens of the newly described species have been deposited in the following institutions: Natural History Museum, London, UK (BMNH), Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France (CIRAD), United States National Museum, Washington D. C., USA (USNM), Canadian National Collection of Insects and other Arthropods, Ottawa, Canada (CNC).

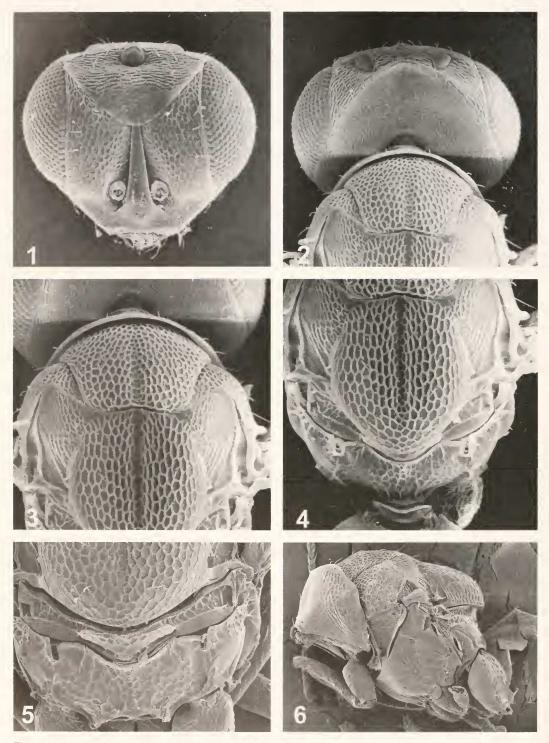
Trisecodes Delvare and LaSalle, new genus (Figs. 1–12)

Name derivation.—A combination of trisuggesting the tarsal formula and -secodes from Asecodes, a genus of Entedoninae. Some members of Asecodes have lines of setae on the forewing which are similar to those seen in Trisecodes. Gender neuter.

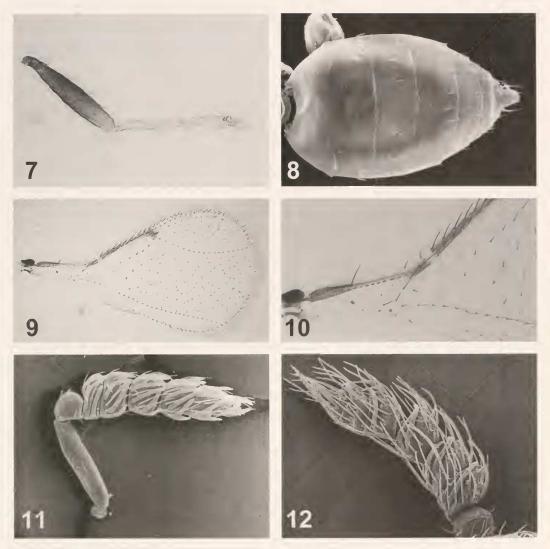
Type species.—*Trisecodes agromyzae* Delvare and LaSalle, new species.

Head (Fig. 1): Frons with distinct scrobal

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Figs. 1–6. *Trisecodes agromyzae*, new genus, new species. 1, head in frontal view; 2, head and basal part of mesosoma in dorsal view; 3, mesonotum; 4, apical part of mesosoma; 5, propodeum in posterior view; 6, mesosoma in lateral view.



Figs. 7–12. *Trisecodes agromyzae*. 7, fore tibia and tarsus; 8, female metasoma in dorsal view; 9, forewing; 10, detail of the base of the forewing; 11, female antenna; 12, male flagellum.

sutures which extend dorsally to the frontal sutures and define a median strip, the strip slightly raised over the surface of the frons and slightly overlapping it laterally. Frontal sutures V-shaped, clearly separated from the median ocellus. Malar sulcus groove like. Clypeus not delimited from lower face. Mandibles bidendate, the teeth acute, of same length. Maxillary palpi bisegmented, labial palpi unisegmented. Labrum strongly bilobed ventrally. **Antenna** (Figs. 11–12): Flagellum with one anellus, a 3-segmented funicle and a 3-segmented clava. Funicular segments transverse, bearing multiporous plate sensilla of two types: usual ones, as found in other Chalcidoidea (elongate sensilla longitudinally oriented with raised and sharp apex) and half-ring ones, embracing each of the segments as well as the apex of the clava; latter sensilla are in oblique or even tranverse orientation (except on third claval segment). Multiporous plate sensilla of the usual type are replaced in males by whorls of long setae. Mesosoma (Figs. 2-6): Pronotum and mesonotum with distinct raised reticulation, same short and very sparse setae, the former narrowly visible dorsally, with its posterior margin deeply emarginate. Mesoscutum and scutellum with distinct median furrow. Notauli complete, straight, of same appearance throughout. Axillae distinctly protruding anteriorly. Scutellum without sublateral furrows or lines, distinctly convex both dorsally and laterally. Propodeum mostly reticulate, with spiracular groove hardly impressed, without subspiracular tubercle, supracoxal flange and nucha. Spiracle formed through incision of the anterior margin of the propodeum, not completely closed. Phragma not reaching the posterior margin of the mesosoma. Prepectus large, reticulate, triangular in lateral view. Mesopleuron convex anteriorly, femoral scrobe reticulate, upper mesepimeron very large, separated from lower mesepimeron by a row of punctures, the latter very small. Metapleuron small but visible, triangular, delimited from the propodeum by a broad, shallow groove. Legs (Fig. 7): All tarsi 3-segmented, segments about of same length. Apical spur of foretibia slightly curved, bifid, the furca at mid length of the spur, the inner branch hardly visible and much shorter than the outer one. Wings (Figs 9-10). Submarginal vein with one dorsal seta. No break between submarginal vein and parastigma, but a hyaline break between parastigma and marginal vein. Forewing with stigmal and postmarginal veins very short. Disc of wing sparsely setose. Hairlines (Rs1 and rm) originating from stigmal vein present. Cubital vein setose and distinct. Metasoma (Fig. 8): Gaster on a transverse petiole, with 7 tergites. Last tergite not subdivided. Cercal hairs on small tubercles.

Trisecodes agromyzae Delvare and LaSalle, new species (Figs. 1–12)

Female.—Length 0.70–0.85 mm. Color: Body, legs except tarsi and antennae dark

with slight bluish reflections. Tarsi whitish. Wings hyaline. Veins dark brown. Head (Fig. 1): Relative measurements (made from a slide mounted specimen): Height 70, width 87, fronto-vertex in front of the median ocellus 48, POL 23, OOL 9, lateral ocelli diameter 7, eyes height 43, width of eye (frontal view) 16, malar space 20, oral fossa 21, antennal toruli-eye distance 14, distance between toruli 10, toruli diameter 7, toruli-lower margin of clypeus length 10. Inner margin of eyes parallel. Malar groove nearly straight as well as genae. Labrum with a row of 4 hairs (one specimen examined). Lower edge of antennal toruli at lower eye margin. One row of 7–8 hairs along inner margin of eye plus one pore. Lower face very faintly squamose, frons reticulate. Upper frons, above frontal sutures, coriaceous (= engraved reticulate), more or less imbricate, vertex with elongate cells which are transversely oriented on its anterior part then oblique. Antenna (Fig. 11): Scape nearly 5 times as long as wide (28:6). Pedicel slightly longer than wide (in lateral view 9:7). First funicular segment very transverse (7: 11), following segments progressively less so. First claval segment slightly transverse (10:12), second one subquadrate, last one elongate (9:5). Each of the flagellar segments bearing 3 ring-like sensilla, in nearly transverse orientation on F1, more oblique in the following segments. Two elongate sensilla at apex of M3 are pincerlike. Mesosoma (Figs. 2-6): Relative measurements: Length 95, width 66, length of mesoscutum 37, of scutellum 45, width of latter 40. Pronotum bearing 3-4 pairs of setae on posterior margin. Mid lobe of mesoscutum bearing 7-8 pairs of short setae laterally. Median furrow on posterior two thirds, smooth on bottom. Scutellum with furrow visible on anterior four fifths. Three pairs of short hairs respectively slightly before and behind mid length of scutellum, last pair, longer, near apex. Dorsellum as a raised reticulate plate. Lateral part of metanotum also reticulate but

sculpturing finer than on dorsellum. Propodeal callus with one short seta. Lower mesepimeron ventrally punctate. Metapleuron smooth. Fore basitarsus with a row of 5 bristly hairs ventrally. Relative measurements on mid leg. Tibia 51, tarsus 40, basitarsus 15 (on dorsal outline), apical spur of tibia 14; latter simple and straight. Measurements of hind leg. Tibia 53, basitarsus 14, apical spur of tibia 7. Forewing (Figs 9–10): Relative measurements: Length 164, width 82, costal cell 45, marginal vein 40, stigmal 5, postmarginal 3, fringe 9. Wing very distinctly widened at apex and regularly rounded. Costal cell with 3-4 dorsal hairs at apex, ventrally bare. Parastigma bearing 2 dorsal hairs, marginal vein with 9-10 dorsal hairs of about twice the width of the vein. A line of 7-8 setae present near anterior wing margin, originating near stigmal vein and extending apically. Basal vein with 2-3 hairs; another one closely beside it. Anal vein (subcubital) represented by a row of 5-6 sparse hairs in front of the retinaculum and more basally by 2-3 isolated hairs behind the basal vein. Basal cell bare. Hind wing: Relative measurements: Length 112, width 33. Wing bearing 3 hamuli, narrowly rounded at apex. Metasoma (Fig. 8): petiole with transverse lamina on anterior margin. Gaster about 1.35 times as long as wide (95:69) on slidemounted specimens. Gastral tergite 1 depressed behind petiole. Tergite 2 with a row of 5 hairs laterally (Fig. 8). Each of the following tergites with one dorsal line of hairs. Ovipositor valvula 70, gonostyli 12. Anterior end of the ovipositor near the base of the gaster. Cercal hairs short, on small tubercles.

Male (Fig. 12).—Length 0.60–0.80 mm. All characters identical but antennal flagellum devoid of elongate sensilla, latter replaced by whorls of long hairs. Only 1, rarely 2, ring-like sensilla on each of the flagellar segments. Gaster length 80, width 45. One long cercal hair. Two long hairs on apex of epipygium.

Material examined.-Holotype 9: BE-LIZE: Cayo Province, Las Cuevas, 550 m, Chiquibul Forest (Lewis O. T.), ex Haplomyza sp. on Senna cobanensis, 27 VIII 1998 (Nº 5649) (Lewis O. T.)(in BMNH). Paratypes (in BMNH, CIRAD, USNM, CNC). Same locality and collector, ex Calycomyza? cassiae on Senna cobanensis, 21 IX 1997 (1 ♂, 4 ♀♀) (Nº 16.040, 16.042, 16.043 & 16.046), 26 IX 1997 (1 2) (Nº 389), 5 XI 1997 (1 ♂) (Nº 1543), 26 VIII 1998 (1 ♂, 1 ♀) (Nº 5573), 29 VIII 1998 (1 ♀) (Nº 5716) and 31 VIII 1998 (1 ^Q) (N^o 5914), 4 IX 1998 (1 \circ) (N^o 6023); 1 \circ , same locality and collector, 5 II 1998 (Nº 1719); same locality and collector, on Stizophyllum riparium, 6 VI 1998 (1 ♂) (Nº 3300), 30 VII 1998 (1 ♂) (Nº 4895); 1 ♂, same locality and collector, ex Nesomyza sp. on Amphilophium paniculatum (N^o 4805); 1 δ , same locality and collector, ex Calycomyza sp. on Triumfetta bogotensis, 6 VII 1998 (Nº 4305); 1 ♂, same locality and collector, on Sida rhombilolia, 11 VIII 1998 (Nº 5342); same locality and collector, ex Calycomyza sidae on Sida acuta, 10 X 1997 (1 ♂, 1 ♀) (Nº 905 & 598), 5 II 1998 (1 ♂, 4 ♀) (Nº 1700, 1701, 1702, 1703 & 1704); 5 IX 1998 (1 º) (Nº 6125). COSTA RICA: Guanacaste, Santa Rosa N. P., 300 m, 25 IV / 16 V 1987 (Janzen D. H. & Gauld I. D.) H-1-O (1 ♂) & H-2-C (1 ♂). GUADELOUPE:, Bouillante, Pigeon, 7 XI 1995, reared from a leaf of Daphnopsis americana mined by Liriomyza schmidti, (Etienne J.)(1 ♀) (N^o 13783/GP 1195).

Distribution.—Belize, Costa Rica and Guadeloupe (Neotropical Region).

Hosts.—Agromyzidae (Diptera) mining plants belonging to various families (Bignoniaceae: *Stizophyllum riparium* and *Amphilophium paniculatum*; Leguminosae: *Sida rhombilolia*; Malvaceae: *Sida acuta* and *S. rhombifolia*; Thymeleaceae: *Daphnopsis americana*; Tiliaceae: *Triumfetta bogotensis*) and belonging to several different genera: *Liriomyza*, *Calycomyza* and *Nesomyza*.

According to O. T. Lewis (pers. comm.), *T. agromyzae* is a larval parasitoid.

Systematic placement.—The combination

of characters exhibited by T. agromyzae does not match any of the currently recognized families of chalcids. Trichogrammatidae is the only family of Hymenoptera having 3-segmented tarsi in both sexes, and it has long been considered to be one of the most easily recognizable and definable families of Chalcidoidea because of this character (Gibson et al. 1999). Additionally, many trichogrammatids have lines of setae on the forewing. On the surface, it would thus appear that Trisecodes should be placed in this family. However, the number of tarsal segments is a reduction character, and a loss of a tarsal segment (5 to 4) is seen many times in the Chalcidoidea in the families Eulophidae, Encyrtidae, Aphelinidae, Mymaridae, Tetracampidae, and even Pteromalidae (LaSalle et al. 1997). It is not inconceivable that the loss of an additional tarsal segment has occured in one of these other lineages. The presence of lines of setae on the forewing radiating from the stigma is also known in several chalcid families: Trichogrammatidae, Eulophidae (Euderinae, Entedoninae), Torymidae and Pteromalidae (Colotrechninae, Ormocerinae: Systasini), and does not restrict a genus to any one family. Moreover, in trichogrammatids, the funicle is at most 2-segmented, the gaster is broadly attached to the mesosoma and the phragma goes into the metasoma, most often deeply so; the frontal sutures are also different from Trisecodes, the mesosoma never has raised reticulation. and the fore tibial spur is simple instead of bifid. Finally all the trichogrammatids whose biology is known are egg parasitoids of various insects.

Despite only having three tarsal segments, we are therefore placing *Trisecodes* in the Eulophidae. Unfortunately, there is little convincing morphological evidence for the monophyly of this family. The combination of 4 tarsal segments and a short, simple fore tibial spur have been considered to be the best characters supporting their monophyly, but LaSalle *et al.* (1997) showed that the tibial spur is more variable than formerly thought. However recent molecular studies (Gauthier *et al.* 2000) demonstrate that Eulophidae when including *Elasmus* does actually represent a monophyletic group.

Many of the derived states found in *Trisecodes* are found in some eulophids (see Table 1). For example the shape and placement of the frontal sutures, the reduced number of tarsal segments, the reduced number of setae on the submarginal vein, the short stigmal vein, the very short postmarginal vein, and the presence of line of hairs on the forewing. The fore tibial spur of *Trisecodes* is also similar to what was recently illustrated for the Eulophidae (LaSalle *et al.* 1997). Eulophidae include finally many larval or/and pupal parasitoids of agromyzid flies.

If we consider the following suite of characters 1) reduced number in antennal segments; 2) special structure of the fore tibial spur; and 3) petiolate gaster with phragma restricted to mesosoma, not entering metasoma, then the unique possibility of familial placement for *Trisecodes* within a currently recognized family of Chalcidoidea is Eulophidae.

Table 1 lists the characters shared by *Trisecodes* with species of Eulophidae according to their subfamilial placement. Some are left unpolarized, others are derived. The table shows that *Trisecodes* shares the largest number of derived similarites with the Entedoninae.

It must however be mentioned that the placement of *Trisecodes* within this subfamily poses problems as it differs from most other entedonines in several important characters. Entedoninae is one of the best defined subfamilies of the Eulophidae (Boucek 1988; Schauff 1991). Support for its monoplyly includes: scutellum with a single pair of setae; submarginal vein with two dorsal setae; mesoscutal midlobe with two pairs of setae; face with frontal sutures distinctly separated from the anterior ocellus; male scape with sensory pores Table 1. Morphological characters of Trisecodes and their distribution in the subfamilies of Eulophidae.

Subfamily Eulophinae	Euderinae	Tetrastichinae	Entedoninae
Character Unporalized characters notauli: many species complete and deep	all species	all species	few species
scutellum general habitus	all species		
mesonotum: many species raised reticulation	most species	very few species	most species
mesopleuron			some species: (see Schauff 1991 fig 81 p. 101)
Derived states antennal segments: all species reduced number	all species	all species	all species
mandibular formula			some species
frontal sutures			most species
anelli: reduced number			many species
mesoscutum: median groove			some species
scutellum: median groove			some species
hairs on propodeal callus: reduced number		many species	many species
hairs on submarginal vein: reduced number		some species	all species
fore tibial spur bifid (LaSalle <i>et al.</i> 1997)	some species (at least)	some species (at least)	some species (at least)
short stigmal vein	most species		all species
short postmarginal vein	most species	most species	most species
lines of hairs figuring Rs1, & r-m	most species		some species
hosts: Agromyzidae several species	a few species	a few species	several species

restricted to the ventral edge; propodeum with a subspiracular tubercle; marginal vein relatively long; stigmal vein relatively short (Boucek 1988; Schauff 1991).

Unfortunately, many of these characters are absent in *Trisecodes*. There are 3 pairs of very small setae on the scutellum, only a single seta on the dorsal surface of the submarginal vein, and no subspiracular spiracle. Also the notauli are complete, another character which is unusual but not unknown in the Entedoninae. However, exceptions are known to all of the characters listed above (see Ubaidillah *et al.* 2000 for some examples), and *Trisecodes* does possess one very strong character to support it as an entedonine, the shape and placement of the frontal sutures. Additionally, one genus of Entedoninae, *Asecodes*, which includes species previously placed in *Teleopterus* (Hansson 1996), may have the forewing with almost identical lines of setae radiating from the stigmal vein. However, it is doubtful that there is a close relationship between *Trisecodes* and *Asecodes* based on other characters, such as the strength of the sculpturing in *Trisecodes*.

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